1e SÉRIE, T. XXXIX, FASC. A, 2002

ISSN: 1105 - 0004

ANNALES GÉOLOGIQUES DES PAYS HELLÉNIQUES

Fondées
Par le Prof. † MAXIME K. MITZOPOULOS

PREMIÈRE SÉRIE

TOME TRENT-NEUVIÈME
FASC. A

ATHÈNES
DÉPARTEMENT DE GÉOLOGIE
Panepistimiopolis, Athènes (157 84)
2002

ΕΘΝΙΚΟΝ ΚΑΙ ΚΑΠΟΔΙΣΤΡΙΑΚΟΝ ΠΑΝΕΠΙΣΤΗΜΙΟΝ ΑΘΗΝΩΝ
ΤΜΗΜΑ ΓΕΩΛΟΓΙΑΣ
UNIVERSITÉ NATIONALE ET KAPODISTRIÈNNE D' ATHÈNES
DÉPARTEMENT DE GÉOLOGIE

NATURAL HISTORY COLLECTION OF VRISA-LESVOS ISLAND

Proceedings of the 1st International Workshop
"On Late Plio/Pleistocene extinction and evolution in the Paleartic. The Vatera site."

September 29-October 2, 1999
Polichnitos, Lesvos Island

ORGANISING COMMITTEE

President:	Prof. Dr. M.D. DERMITZAKIS
Vice-President:	Prof. P.Y. SONDAAR
Secretary:	Dr. H. DRINIA
Treasurer:	Ass. Prof. F. POMONI - PAPAIOANNOU
Member:	Dr. J. DE VOS

Sponsored by:
Ministry of Aegean - Prefecture of Lesvos - G.S.R.T. & Municipality of Polichnitos

THE PRIMITIVE HORSES OF THE VATERA FORMATION (LESVOS, GREECE)*

by

VERA EISENMANN**

I. INTRODUCTION

Monodactyl equids (genus *Equus*), still represented today by zebras, asses, hemiones, and true (caballine) horses, are known in Eurasia since 2.5 Ma. Extant species of *Equus* and fossil species younger than about 1 Ma have in common basicranial proportions different from those observed in older taxa (EISENMANN & BAYLAC, 2000); they may form a monophyletic group. The older European taxa commonly referred to as 'stenonoid' are probably not ancestral to recent *Equus*; their monophyly is questionable since their grouping is based on a symplesiomorphy: the rounded, 'stenonine', shape of the double knot. In some cases, this allegedly stenonine shape comprises so many different morphologies that the character should rather be mentioned as 'not-caballine'. In this paper these stenonoid horses will be referred to as 'primitive'.

Among primitive horses, several forms can be recognized as monophyletic because they share a deep narial notch apparently absent in older, plesippine, forms. These are *E. stenonis* (found at Valdarno, Saint-Vallier, La Puebla de Valverde, and Kuruksai), the smaller and somewhat different form of Gerakarou, and the larger and somewhat different forms of Khapry and Nihowan. The subspecies of *E. stenonis* also share some other characters (as medium size, not very long protocones, rounded double knots, relatively flat distal metapodials) neither of which is specific. Let us stress that when skulls are unknown, such teeth and bones are referred to *Equus stenonis* only because of their geographical and chronological contexts (if there is no context, it is nearly impossible to tell whether a bone or tooth of *Equus* belongs to an extant species or to a taxon 2 Ma old). Another group, possibly related to older plesippine North-American equids (like *E. shoshonensis*) is yet poorly known (no skulls in Europe nor in Africa). In that group, the limb bones are slenderer and deeper (like in the North-African *E. numidicus*), and the limb bones proportions more cursorial. The two groups seem to coexist during the Pliocene and the Early Pleistocene.

The faunal list of Vatera indicates an Upper Pliocene context. Comparisons and

---

* Τα πρωτόγονα άλογα του Σχηματισμού Βατερών (Λέσβος).

** UMR 8569 and ESA 8045 of the CNRS, Laboratoire de Paléontologie, 8 rue Buffon, 75005 Paris, France. E-mail : vera@mnhn.fr.

discussions of the available equid material will accordingly be made with primitive horses of that age.

In addition to a classical biometrical description of the Vatera material, the present article presents a technique of size assessment applied to Vatera horses in comparison with various *E. stenonis*; a tentative morphometric characterization of primitive metapodials, and a tentative grouping of primitive horses according to this characterization; a brief review of the cases of coexistence of two primitive horses in association with *Nyctereutes* or *Canis*.

II. THE VATERA MATERIAL

There are about 40 specimens of *Equus* including one lower fragmentary cheek tooth. They come from different localities. At the 'Electric Site' (E Site) was first found a talus (PO 1); subsequent excavations have produced a third metatarsal (PO 5) and a femoral diaphysis, possibly juvenile (PO 6). The 'F Site' was discovered because fossils were found nearby a bulldozer trenching. Among these bones, one distal tibia (PO 94), one talus and one calcaneum (PO 95 and 96), another talus (PO 123), one lateral metatarsal (PO 91) and a broken lower cheek tooth (PO 65) belong to horses. A country man found two first phalanges (PO 92 and PO 93). The other bones were excavated at the F Site in situ. The bones are usually well preserved and often associated (right hind leg PO 212; left talus PO 101 and calcaneum PO 129).

The talus (PO 1) and third metatarsal (PO 5) found at the 'Electric Site' as well as two specimens collected near the bulldozer trenching (PO 93 and 123) are larger than the other bones. The differences in size are illustrated below by applying the technique of the 'Variability Size Index (VSI)'. For the moment, we will leave them apart and describe the main part of the material which belongs to the smaller horse.

III. DESCRIPTION OF THE SMALLER *EQUUS* (TABLES 1 TO 4)

Limb segments

The relative lengths of proximal and distal segments of *Equus* limbs are different in cursorial and less cursorial forms (EISENMANN, 1984). In cursorial forms, the metapodials are longer relative to humerus, femur, radius, and tibia. When compared to (the very cursorial) *E. hemionus onager* (zero absciss line in Figure 1), the corresponding parts of the diagram tend to be more parallel to the absciss in more cursorial forms (Venta Micena and Vatera) than in less cursorial (El Rincón and Saint-Vallier). Moreover, first phalanges (and particularly posterior first phalanges) are relatively long at El Rincón and Saint-Vallier. The same is true at La Puebla de Valverde (EISENMANN, 1999, table 5), Sesklo (ATHANASSIOU, 2001), and probably in all *Equus stenonis*.

Metapodials

The unique MC III is as long as the metacarpals of El Rincón but slenderer (Figure 2). Five MT III are intermediate between those of El Rincón (EISENMANN, 1999) and La Puebla de Valverde (Table 3, Figure 3).

Table 1

	RADIUS	TIBIA	TIBIA
	PO 23	PO 94	PO 212
Greatest length	[353]		[374]
Mid-shaft breadth (DT)	43,0	[46]	45,0
Mid-shaft depth (DAP)	30,5	[30]	32,0
DT distal maximal	81,0	75,0	70,0
DT distal articular	69,0		
DAP distal articular	38,0		52,0
	HUMERUS	FEMUR juv ?	FEMUR
	PO 23	PO 6	PO 212
Mid-shaft breadth (DT)	39,0	34,5	40,0
DT distal			[99]

Table 1. Measurements in millimeters of proximal limb bones of Vatera.

Table 2

TALUS	PO 1	PO 95	PO 101	PO 212	PO 123
Greatest length	73,0	63,0	70,0	63,0	73,0
Medial length of trochlea	74,0		69,0	64,0	74,0
Greatest breadth (DT)	74,0	65,0	64,0	61,0	75,0
Trochlear DT	34,0	28,0	30,0	31,0	33,5
DT articular distal	61,0	51,0	54,0	52,2	61,0
DAP articular distal	43,5	37,0	38,5	36,5	43,0
Medial depth (DAP)	61,5		57,0	53,0	61,0
CALCANEUM	PO 151 juv	PO 96	PO 129	PO 212	
Greatest length	[110]	121,0	117,5	[120]	
Length of proximal part		82,0	83,0	81,0	
Minimal breadth (DT)	24,0	22,0	23,0	22,0	
DT proximal		32,0	35,0	35,0	
DAP proximal		52,0	49,0	52,0	
DAP distal	58,0	57,0	54,0	55,0	
DT distal	55,0	56,0	57,0		

Table 2. Measurements in millimeters of tarsal bones of Vatera.

Table 3

THIRD METACARPAL AND METATARSALS		MC	MT	MT	MT	MT	MT	MT
		PO 121	PO 5	PO 110	PO 118	PO 136 juv	PO 212	PO 446
Greatest length	1	253,0	315,0	290,0	282,0	282,0	280,0	288,0
Mid-shaft breadth (DT)	3	36,1	42,0	36,0	34,0	31,0	35,2	36,2
Mid-shaft depth (DAP)	4	28,5	38,3	32,0	32,5	28,0	33,0	33,9
DT proximal	5	55,9	66,0		51,0	51,0	51,0	54,0
DAP proximal	6	35,2			45,0		43,5	45,7
DT articular facet for carpale/tarsale III	7	46,5			46,5		47,0	52,0
DT articular facet for carpale/tarsale IV	8	16,2			13,0		13,5	14,0
DT distal maximal	10	52,0	58,0	52,0	51,0	50,2	49,0	51,8
DT distal articular	11	50,7	58,0	50,5	49,0		50,5	50,0
DAP distal maximal	12	38,7	44,1	40,0	39,0		38,5	
Medial condyle DAP minimal	13	30,2	35,0	30,0	30,0		29,0	28,0
Medial condyle DAP maximal	14	32,5	36,7	33,0	31,0		31,0	31,0
FIRST ANTERIOR AND POSTERIOR PHALANGES		juv ?	A	A	P	P		MT
		PO 92	PO 93	PO 132	PO 111	PO 212		PO 444
Greatest length	1	88,0	87,5	85,0	82,0	78,0		[300]
Mid-shaft breadth (DT)	3	32,0	37,2	31,7	34,0	34,0		
DT proximal	4	50,0	55,0	[50]	55,0	56,0		
DAP proximal	5	36,5	37,5	[37]	40,0	41,0		
DT distal maximal	6	44,0	49,5	42,7	44,0	45,3		
Greatest length of trigonum phalangis	7	55,0	56,0	48,0	50,0	43,0		
Supratuberosital length	10	67,0	62,0	59,0	56,0	53,0		
Infratuberosital length	12	14,0	15,0	16,0	18,0	18,0		
DT distal articular	14	46,0	47,0	44,5	44,0	43,2		

Table 3. Measurements in millimeters of distal limb bones of Vatera. MC = third metacarpal, MT = third metatarsal, juv = juvenile, A = anterior, P = posterior.

Table 4

SECOND PHALANGES	A	A	P	P
	PO 132	PO 205	PO 112	PO 212
Greatest length	45,5	48,0	50,0	48,0
Anterior length		36,0	39,0	35,0
Mid-shaft breadth (DT)	43,0	45,1	42,0	41,5
DT proximal	50,0	52,0	50,0	53,5
DAP proximal	31,0	33,0	34,0	34,5
DT distal	45,0	49,0	46,0	43,5
THIRD PHALANGES			P	P
			PO 112	PO 212
Greatest length				50,0
Anterior length				54,0
Anteroposterior diameter (DAP)				59,0
Height				41,0
Transverse diameter (DT)				61,0
DT of the articular facet			[45]	42,5
DAP of the articular facet			30,5	27,0
Circumference of the sole				146,0

Table 4. Measurements in millimeters of second and third phalanges of Vatera. A = anterior, P = posterior.

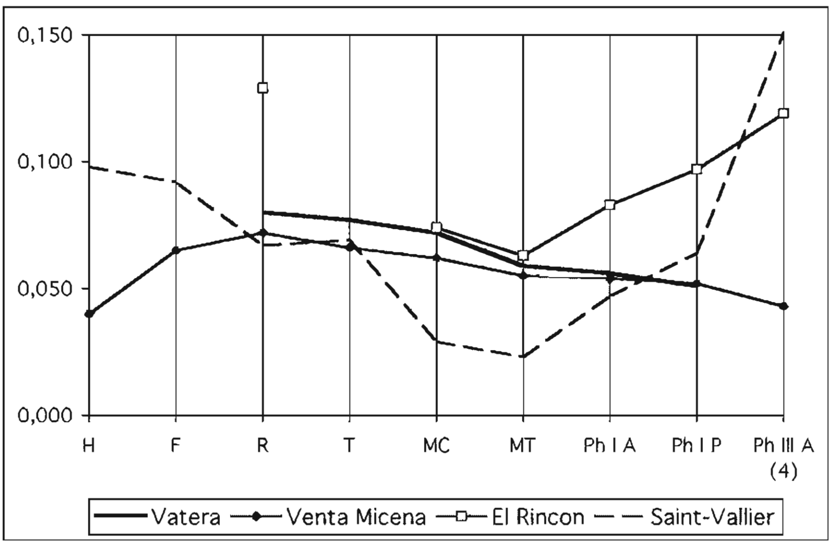

Fig. 1. Ratio diagram of limb bones proportions in fossil *Equus* compared to the extant *Equus hemionus onager* (reference line). Lengths of humerus (H), femur (F), radius (R), tibia (T), third metacarpal (MC), third metatarsal (MT), first anterior phalanx (Ph I A), first posterior phalanx (Ph I P), and breadth of third anterior phalanx (Ph III A (4)).

Table 5

LIMB BONES BREADTHS OF *E. stenonis vireti* OF SAINT-VALLIER					
	x	s		x	s
Humerus minimal	39,2	1,44	Femur minimal DT	43,9	2,56
Humerus distal maximal	82,1	2,35	Tibia distal maximal DT	80,5	3,00
Radius proximal articular	81,0	3,95	Talus distal articular DT	54,7	2,96
Radius distal articular	68,8	2,61	Calcaneum proximal DT	36,7	1,91
MC proximal articular	54,8	1,74	Calcaneum distal DT	56,2	1,88
MC distal articular	51,0	1,58	MT proximal articular DT	53,5	1,98
PhIAP minimal	35,7	2,21	MT distal articular DT	51,1	1,48
PhIAP distal maximal	48,5	2,04	PhIIIAP articular DT	49,5	2,50
PhIIAP minimal	47,4	2,21			

Table 5. Means and standard deviations (in millimeters) of bone breadths in *Equus stenonis vireti* of Saint-Vallier.

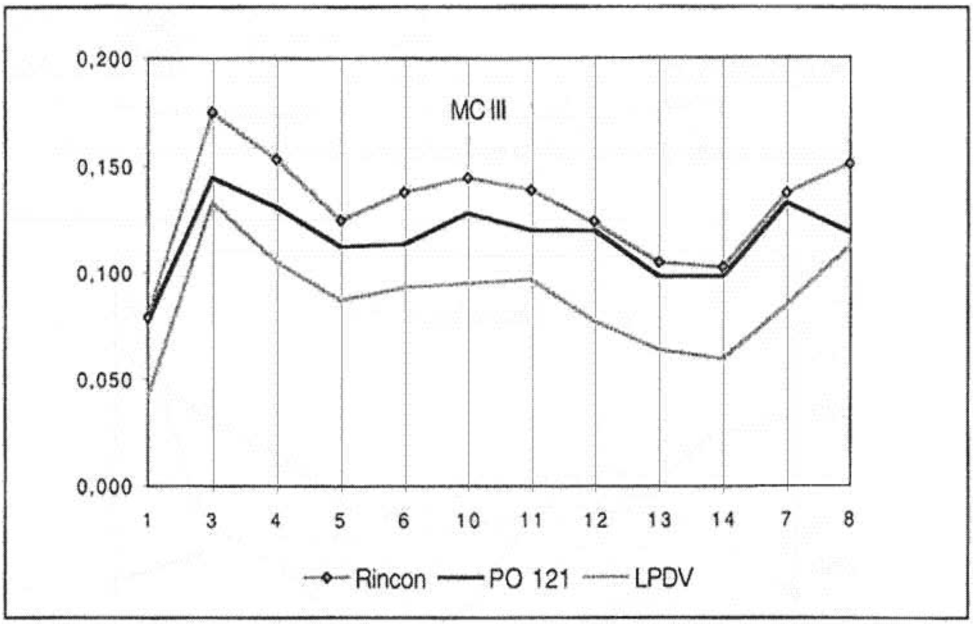

Fig. 2. Ratio diagram of average third metacarpal measurements of *E. stenonis* of El Rincón and La Puebla de Valverde compared with one specimen of the small *Equus* of Vatera. The reference line is *Equus hemionus onager*. 1 = maximal length; 3 = breadth at mid-diaphysis; 4 = antero-posterior diameter (APD) at mid-diaphysis; 5 = proximal breadth; 6 = proximal APD; 10 = distal breadth at the supra-articular tuberosities; 11 = distal articular breadth; 12 = maximal APD of the keel; 13 = minimal APD of the medial condyle; 14 = maximal APD of the medial condyle; 7 = diameter of the articular facet for the magnum; 8 = diameter of the anterior articular facet for the unciform.

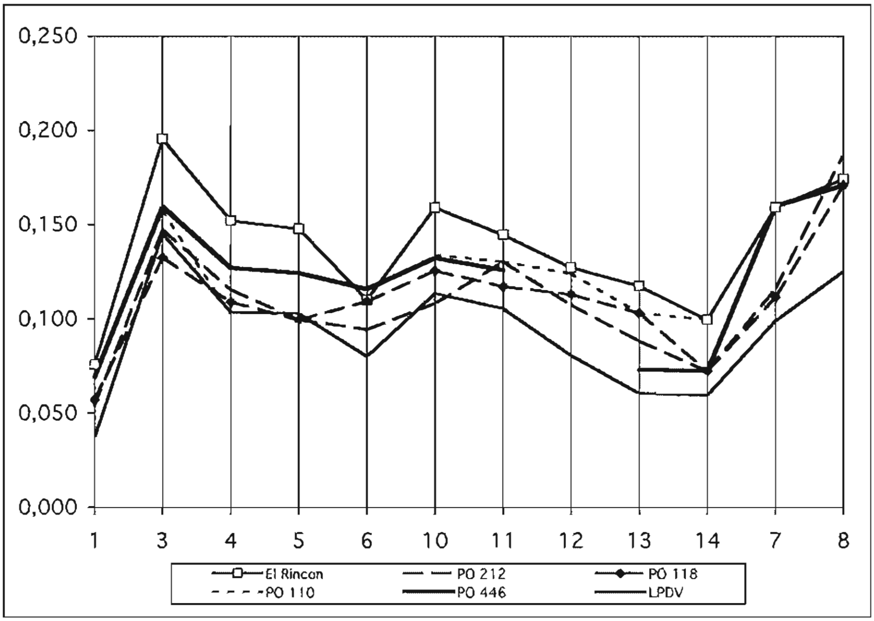

Fig. 3. Ratio diagram of average third metatarsal measurements of *E. stenonis* of El Rincón and La Puebla de Valverde compared with four specimens of the small *Equus* of Valera. The reference line is *Equus hemionus onager*. Same codes as in Figure 2, except 7 = diameter of the articular facet for the large cuneiform; and 8 = diameter of the articular facet for the cuboid.

First Phalanges

Anterior phalanges (PO 92 and 132) are intermediate in length between El Rincón and La Puebla de Valverde but slenderer than any of these two samples (Figure 4). Posterior phalanges (PO 111 and 212) are about the length of La Puebla de Valverde but more robust than either at El Rincón or La Puebla de Valverde (Figure 5).

IV. RELATIVE SIZE, BODY WEIGHT, AND WITHER'S HEIGHT

1. Relative size

Equus bones do not evidence sexual dimorphism, at least not in a marked way. The distribution of metrical values inside a monospecific adult (epiphyses perfectly fused) sample is normal. In consequence, the occurrence of more than one species in a given sample may be detected once the normal intraspecific size variability is known. Such occurrences may reflect an artificial mixing of chronologically different strata or the actual coexistence of different taxa at the same time. The coexistence of two species of equids may possibly give some biochronological indications.

The Variability Size Index (VSI) is one of the size index scaling techniques used by archeozoologists (UERPMANN, 1982; MEADOW, 1999). A sample including all the bones of a taxon is choosen as reference. Mean and standard deviation are calculated for each measurement of this sample. The comparisons are done using the following formula: VSI = 25(x-m)/s where s is the standard deviation of the mean (m) of the

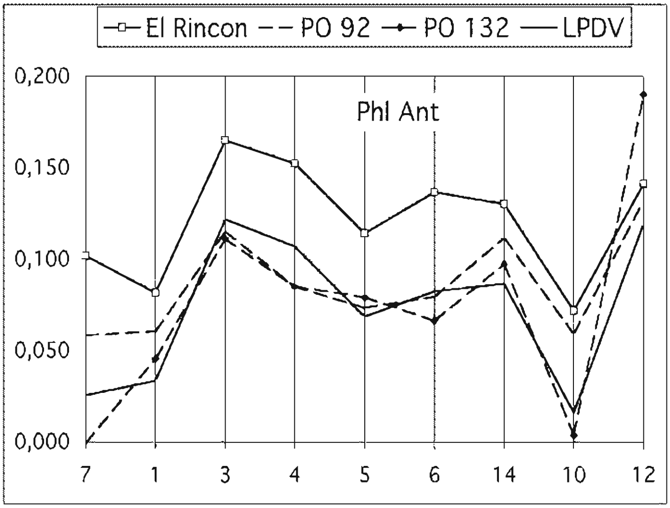

Fig. 4. Ratio diagram of average first anterior phalanges measurements of *E. stenonis* of El Rincón and La Puebla de Valverde compared with two specimens of the small *Equus* of Vatera. The reference line is *Equus hemionus onager*. 1 = maximal length; 3 = breadth at mid-diaphysis; 4 = proximal breadth; 5 = proximal antero-posterior diameter; 6 = distal breadth at the supra-articular tuberosities; 7 = greatest length of trigonum phalangis; 10 = medial supratuberosital length; 12 = medial infratuberosital length; 14 = distal articular breadth.

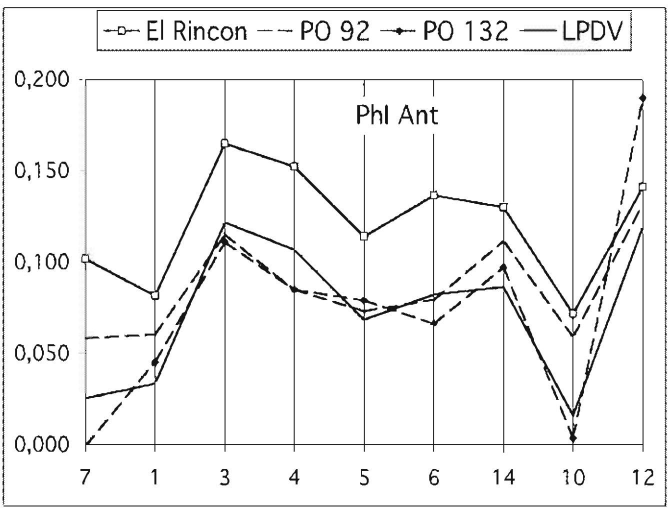

Fig. 5. Ratio diagram of average first posterior phalanges measurements of *E. stenonis* of El Rincón and La Puebla de Valverde compared with two specimens of the small *Equus* of Vatera. The reference line is *Equus hemionus onager*. Same codes as in Figure 4.

reference measurements to which another measurement (x) is being compared. The obtained values are plotted on a histogram graduated in one, two, three, or more standard deviations from the reference. As phrased by MEADOW (1986), 'Using this formula, the standard dimension is set at zero; a measurement one standard deviation larger than the standard (reference) dimension will be plotted at 25, one standard deviation smaller at –25, etc'.

I have chosen the sample of *Equus stenonis vireti* of Saint-Vallier as reference. I considered only the bone breadths (one measure by bone, excluding juvenile specimens). Means and standard deviations are given in Table 5. On Figure 6, the breadths of all these bones appear normally distributed on each side of the 0 axis. The distribution is also normal for the sample of La Puebla de Valverde. It is not normal for the sample of Senèze in which several taxa of horses are certainly represented. The histogram for Vatera evidences also the presence of more than one taxon: most of the material found at the F Site belongs to a horse about the size of La Puebla de Valverde (Figure 6) and Sesklo (Figure 9); it is the smaller *Equus* described above. The bones found at the E Site and some bones collected near F Site are the size of the largest specimens of Senèze, or intermediate.

2. Body weight

A previous paper (EISENMANN & SONDAAR, 1998) discussed several technics of body weight evaluation in equids. Reasonable estimations may be obtained by applying the following formulas: Ln of the weight = –4.525 + 1.434 (Ln of the product of MC10 by MC13), and = –4.585 + 1.443 (Ln of the product of MT10 by MT13).

Ln is the natural logarithm, MC10 and MT10 are the distal supra-articular widths of the third metacarpal and metatarsal, MC13 and MT13 are the distal minimal depths of the medial condyles of the same bones.

Estimations based on the unique third metacarpal and on the mean of six metatarsals of the smaller horse of Vatera indicate body weights around 415 Kg and 408 Kg respectively (close to an average Grevy's zebra). The body weight estimated from the unique very large metatarsal is about 605 Kg (close to a small Draft horse).

3. Wither's height

As discussed in a previous paper (EISENMANN, 2000), the well known 'Kiesewalter indices' are not adapted to all and every kind of equid because their limb bones proportions may differ. Among the extant equids, Grevy's zebras have the closest proportions (between radius, tibia, third metacarpal, and third metatarsal) to those of the smaller horse of Vatera. The corresponding indices suggest for the latter a wither's height between 155 and 158 cm (close to a Thoroughbred). No wither's height may be suggested for the large Vatera horse.

V. DESCRIPTION OF THE LARGE *EQUUS*

Two tali (PO 1 and 123, Table 2) are larger than the tali of Saint-Vallier (DERMITZAKIS *et al.*, 1991), about the size of those of Loubières de Pardines.

One metatarsal (PO 5, Table 3) is quite larger than the specimens of La Puebla de Valverde and even El Rincón (Figure 7), about the size of a specimen of Khapry and of some specimens of Livenzovka. It is quite robust, much more so than the other, smaller,

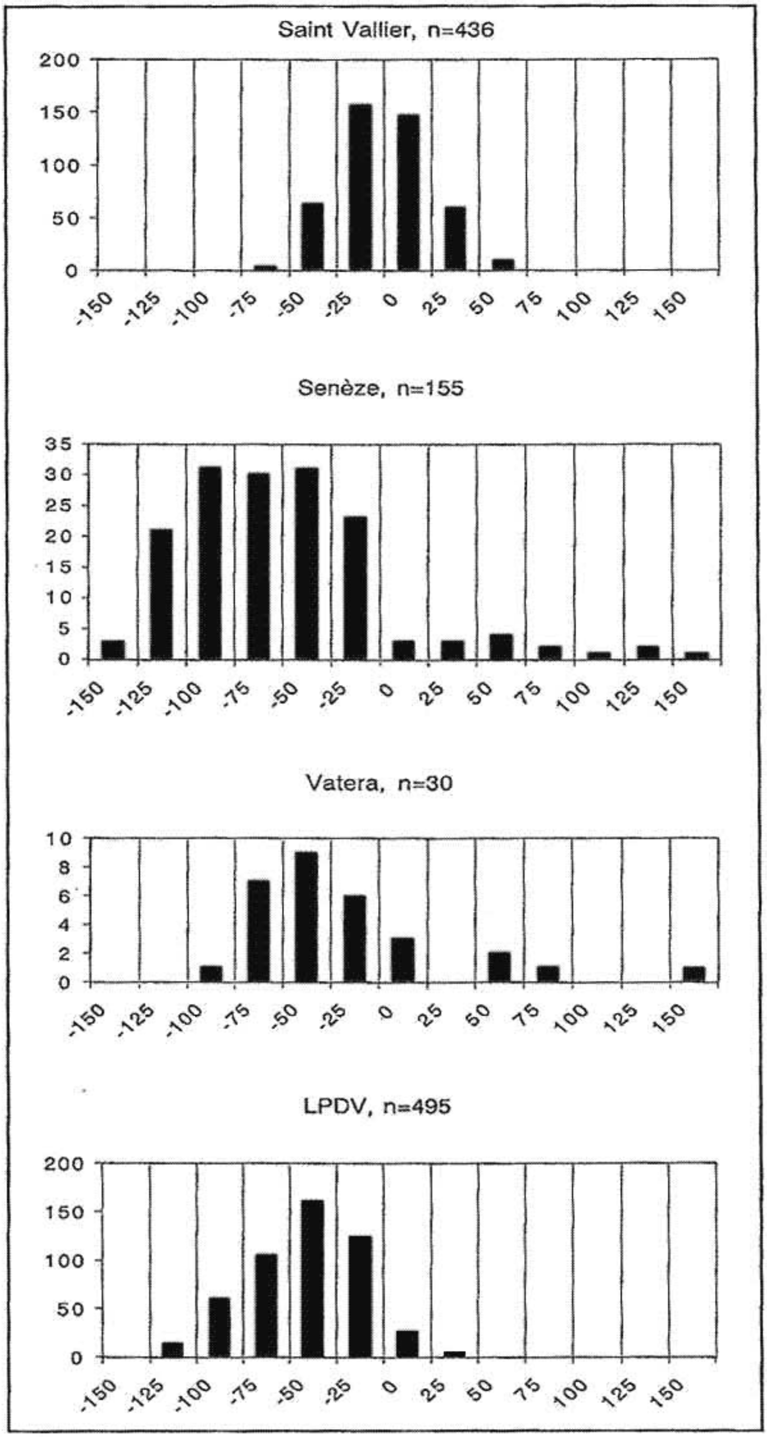

Fig. 6. Variability Size Indices of various primitive horses ; n = number of bone breadths.

metatarsals of Vatera.

The MTIII PO 5 and the tali PO 1 and 123 plot apart from the main histogram on the Variability Size Index diagram (Figure 6).

One first phalanx (PO 93, Table 3) is very close to first anterior phalanges of Saint-Vallier, much more robust than the phalanges of El Rincón (Figure 8) and than the other phalanges of Vatera. On the VSI diagram, it plots with the biggest specimens of the main sample of Vatera.

The large form is not well represented and there is even a size gap between the very large metatarsal and the other big bones (Figure 6). It is interesting to note that this gap is filled by the late Pliocene *Equus* of Sarikol Tepe (KOSTOPOULOS & SEN, 1999). The Variability Size Index (Figure 9) shows that the Sarikol Tepe and Vatera large horses were probably larger than the forms of Montopoli, Saint-Vallier, and El Rincón. The material is, however very poor.

VI. STENONINE METAPODIALS: TENTATIVE CHARACTERIZATION

Statistical descriptions of primitive metapodials were published elsewhere (EISENMANN, 1979, 1999; EISENMANN & KARCHOUD, 1982). Although the use of indices is objectionable (FORSTEN, 1982), some basic features may conveniently be expressed by indices, and used as guides in a first approach. The samples of El Rincón, La Puebla de Valverde, Saint-Vallier, Chilhac, Olivola, and Matassino were used as reference for *E. stenonis* (Table 6). The same indices were calculated for several other localities using also personal data. In addition were used data on the Chinese localities of Bajiazui and Weinan communicated by DENG TAO (1997, 1999); on the Greek localities of Dafnero (KOUFOS & KOSTOPOULOS 1993) and Sesklo (ATHANASSIOU, 2001), communicated by KOUFOS and ATHANASSIOU; on the French locality of Peyrolles and the Romanian locality of Tetoiu published by SAMSON (1975).

1. Robustness

The robustness can be expressed by an index (100 × minimal breadth of diaphysis / maximal length). Robustness is somehow related to humid conditions. In third metacarpals (MC III) of the above mentioned forms, the average robustness indices fall in between 15 and 16,5 (they are exceptionally less than 14). In third metatarsals (MT III), they fall in between 13 and 14, and are exceptionally less than 12.

Table 6

	E. stenonis	PO 5	PO 121	PO 110	PO 118	PO 212	PO 446	Gerakarou
Average MC robustness	14.9-16.3		14.3					13.7
Average MC diaphysis depth	73.3-77.7		78.9					81.9
Average MC distal flatness	162.1-168.7		160					156.6
Average MT robustness	13-14	13.3		12.4	12	12.6	12.5	11.7
Average MT diaphysis depth	90.6-92.6	91.2		88.9	95.6	93.8	93.6	92.8
Average MT distal flatness	157-167.3	155.9		157.6	164.5	158	167	150.6

Table 6. Average metapodial indices in *E. stenonis* of El Rincón, La Puebla de Valverde, Saint-Vallier, Chilhac, Olivola, and Matassino compared to Vatera metapodials.

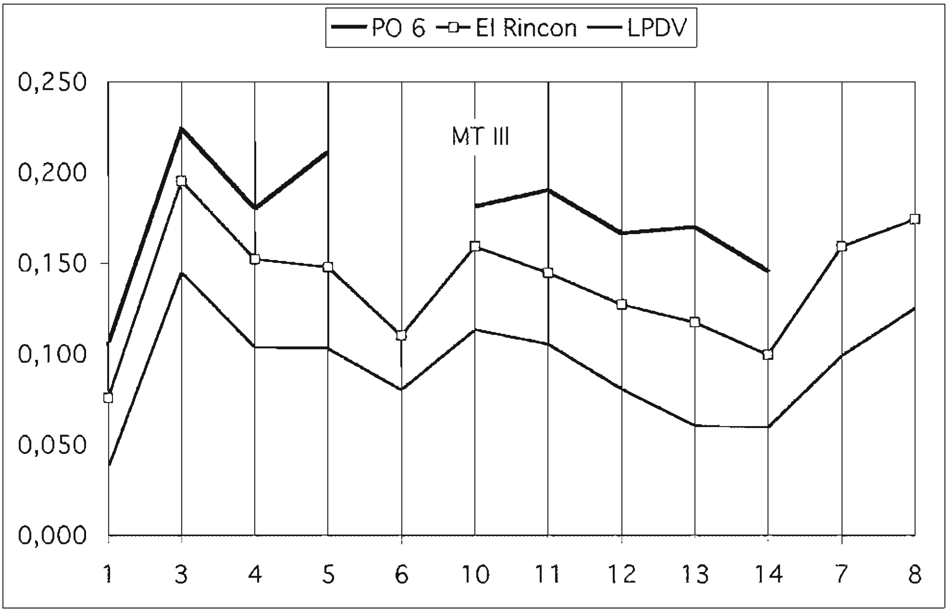

Fig. 7. Ratio diagram of average third metatarsal measurements of *E. stenonis* of El Rincón and La Puebla de Valverde compared with one specimen of the large *Equus* of Vatera. The reference line is *Equus hemionus onager*. Same codes as in Figure 3.

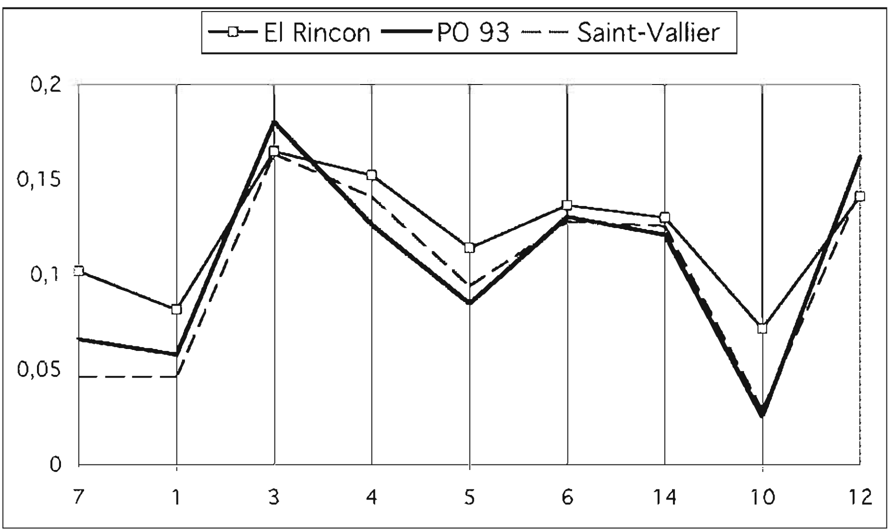

Fig. 8. Ratio diagram of average first anterior phalanges measurements of *E. stenonis* of El Rincón and Saint-Vallier compared with one specimen of the large *Equus* of Vatera. The reference line is *Equus hemionus onager*. Same codes as in Figure 4.

2. Depth of diaphysis

Robust bones are often flater than gracile bones. In the stenonine forms listed above, the average depth indices (100 × antero-posterior diameter of diaphysis / minimal breadth of diaphysis) are in general comprised between 73 and 78 in MC III and between 90 and 93 in MT III.

3. Flatness of the distal end

Flat diaphyses are usually associated with flat distal ends. In the stenonine forms listed above, the average flatness indices (100 × supra-articular distal breadth / greatest antero-posterior diameter of the medial condyle) are larger than 162 (between 162 and 169) in the MC III, and larger than 157 (between 157 and 167) in the MT III.

According to these criteria, the large *Equus* of Vatera resembles *E. stenonis*, while the smaller form does not, except for the distal flatness of the MT III (Table 6).

VII. *E. STENONIS* AND OTHER PRIMITIVE HORSES

Figures 10-13 attempt to visualize the grouping of various subspecies of *E. stenonis* in comparison to the grouping, or lack of grouping, of other *Equus* of about the same age or older. The horses of Livenzovka are not included because the material probably comes from different levels of uncertain age (FORSTEN, 1998). Neither are included the Senèze horses probably originating from different levels (see above), nor *Equus stehlini* and similar forms which are believed younger (TORRE *et al.*, 1996). Although probably also younger, *Equus granatensis* of Venta Micena is included because of its resemblance to one of the horses of Huelago (EISENMANN, 1999). Table 7 lists the studied localities, the symbols used for them in Figures 10-13, their assumed ages, and the corresponding bibliographical references. Figures 10 and 11 combine lengths and indices of robustness of the metapodials; Figures 12 and 13 combine indices of diaphyseal depth and of distal flatness. Symbols for localities with *E. stenonis* (letters) and assumed *E. stenonis* (numbers) are intentionally printed larger and in bold characters.

Figures 10 and 11 evidence the great length of the metapodials from Huelago (partim), Khapry, Morskaja, Oasele, Podpusk, Tataourova, Tegelen, and of the large metatarsal from Vatera. Since all these forms are represented by very few bones, the interpretation of their position relative to the other groups is difficult. It seems certain, however, that the metapodials of Huelago (partim), Khapry, Podpusk, and Tegelen do not belong to *E. stenonis*.

Naturally enough, reference localities for *E. stenonis* (El Rincón, La Puebla de Valverde, Saint-Vallier, Chilhac, Olivola, and Matassino) appear grouped on all diagrams. To the same group belong metapodials of Dafnero, Dmanisi II, East Turkana (partim), Fuentenueva 1, Huelago (partim), Kotzakhuri, Kuruksai, Loubières de Pardines, Montopoli, Olduvai (partim), Peyrolles, Sarikol Tepe, Valdarno (partim), Tetoiu, and Weinan. Metapodials of Sesklo (symbol 12) have an extreme position. Fragments of metacarpals from Omo and Aïn Jourdel (not illustrated) probably belong also into this group.

Other, slenderer, metapodials form another group. Those come from Hagerman, Bajiazui, Aïn Boucherit, Aïn Jourdel (partim), East Turkana (partim), Olduvai (partim), Omo (partim), Tsalka, Venta Micena, and probably Huelago (partim). For simplicity sake, they are referred to as *Equus numidicus*-like. The metacarpal of

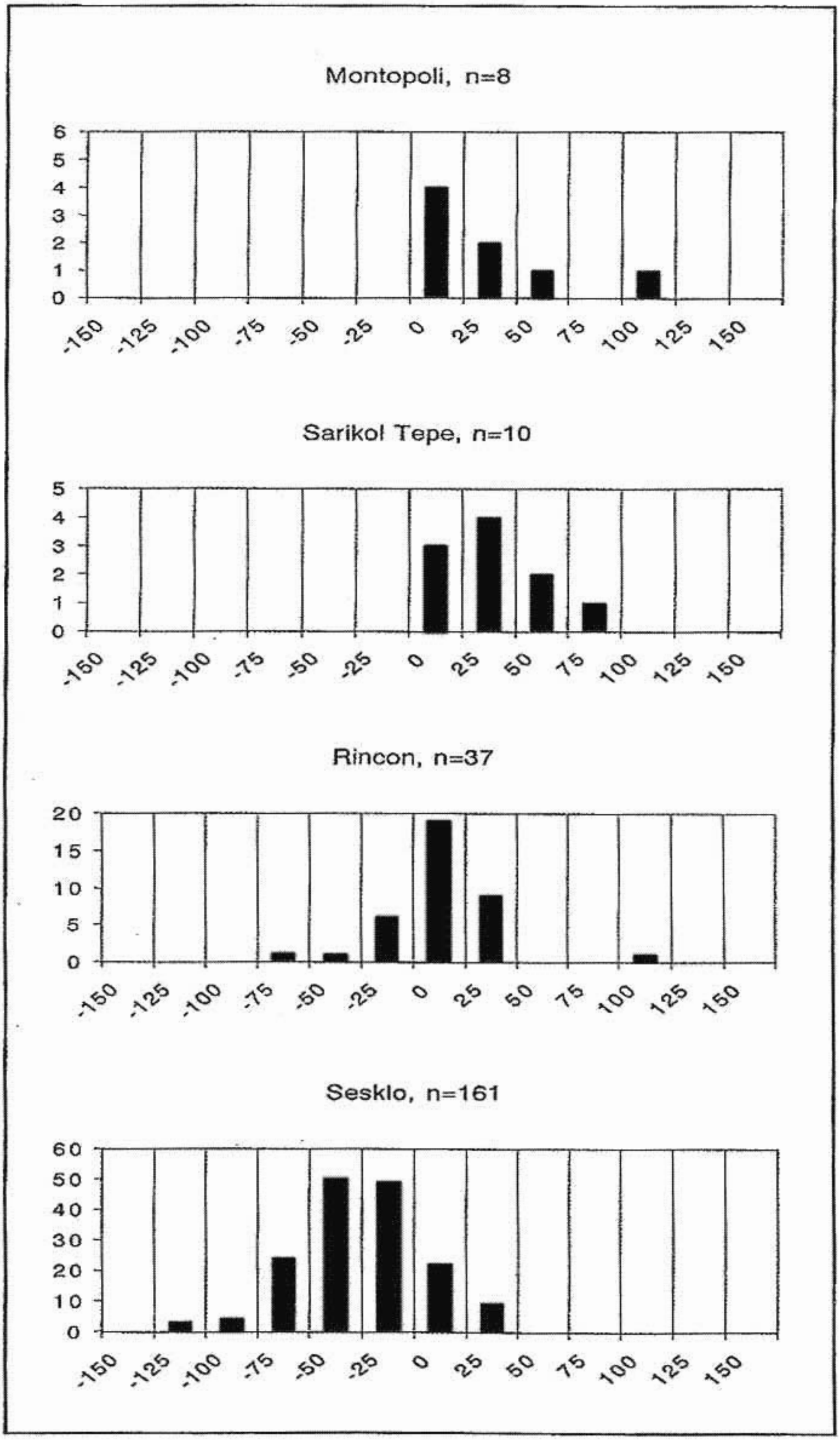

Fig. 9. Variability Size Indices of various primitive horses ; n = number of bone breadths.

Table 7

LOCALITIES	Symbols	AGE	REFERENCES
Aïn Boucherit, *E. numidicus*	AB	about 1.8 Ma ?	
Aïn Jourdel, *E. numidicus*	16	about 2.5 Ma	GERAADS et al. 1986
Bajiazui, E. cf. *shoshonensis*	Ba	about 2.5 Ma	DENG TAO 1997, 199
Chilhac, *E. stenonis*	Ch	older than Saint-Vallier	BŒUF 1997
Dafnero, *E. stenonis*	1	Saint-Vallier Faunal Unit	KOUFOS & KOSTOPOULOS 1997
Dmanisi II, *E. stenonis*	2	younger than Dmanisi IV-V	GABUNIA & VEKUA 1995
Dmanissi IV-V	22	about 1.7 Ma	GABUNIA & VEKUA 1995
East Turkana area 105, *E. stenonis*	23	partly below Olduvai event	BROWN et al. 1985, 1986
East Turkana area 100, *E. numidicus*	17	partly below Olduvai event	BROWN et al. 1985, 1986
Fuentenueva 1, *E. stenonis*	3	Saint-Vallier	ALBERDI & RUIZ BUSTOS 1989
Hagerman, *E. shoshonensis*	Ha	about 3.4 Ma	LUNDELIUS et al. 1987
Huelago, *E.* cf. *numidicus*	Hu	Montopoli Faunal Unit	ALBERDI et al. 1998
Huelago, *E. stenonis*	4	Montopoli Faunal Unit	ALBERDI et al. 1998
Khapry	Kh	MN 17	SOTNIKOVA 1989
Kotzakhuri, *E. stenonis*	5	above Olduvai event	GABUNIA & VEKUA 1995
Kuruksai (loc 73), *E. stenonis*	6	below Olduvai event	DODONOV et al. 1991
La Puebla de Valverde, *E. stenonis*	LP	about Saint-Vallier	ALBERDI et al. 1998
Matassino, *E. stenonis*	Ma	1,8 Ma	TORRE et al. 1996
Montopoli, *E. stenonis*	7	just above Gauss	TORRE 1987
Morskaja	Mo	Khapry complex	GROMOVA 1949
Oasele	Oa	about Montopoli Faunal Unit	SAMSON 1975
Olduvai Bed I, *E.* cf. *numidicus*	18	2 - 1.7 Ma	TAMRAT et al. 1995
Olduvai Bed I, *E.* cf. *stenonis*	8	2 - 1.7 Ma	TAMRAT et al. 1995
Olivola, *E. stenonis*	Ov	about Olduvai event	AZZAROLI et al. 1997
Omo G, *E. numidicus*	19	2.3 - 1.8 Ma	BROWN et al. 1985
Loubières de Pardines, *E. stenonis*	9	Saint-Vallier	HEINTZ 1970
Creux de Peyrolles, *E. stenonis*	10	younger than Saint-Vallier	HEINTZ 1970
Podpusk	Pd	2.4 - 2 Ma	ALEKSEEV 1997
El Rincon, *E. stenonis*	R	Montopoli Faunal Unit	ALBERDI et al. 1998
Saint-Vallier LD3, *E. stenonis*	SV	2 Ma	BOUCHEZ et al. 1984
Saint-Vallier LD2, *E. stenonis*	20	below the classical level	DEBARD et al. 1994; VALLI, pers. com.
Sarikol Tepe, *E. stenonis*	11	Late Pliocene	KOSTOPOULOS & SEN 1999
Sesklo, *E. stenonis*	12	Lower MN 17	ATHANASSIOU 2001
Tataourova	Ta	Earliest Pleistocene	VANGENHEIM com. pers.
Tegelen	Tg	about 1.8 Ma or older	WESTERHOFF et al. 1998
Tetoiu, *E. stenonis*	13	Upper Saint-Vallier zone	RADULESCO & SAMSON 1990
Tsalka, *E.* cf. *numidicus*	21	above Olduvai	GABUNIA & VEKUA 1989
Valdarno, *E. stenonis*	14	Olivola Faunal Unit	DE GIULI 1972
Vatera large	V1	Lower MN 17 ?	
Vatera small	V2	Lower MN 17	
Venta Micena, *E. granatensis*	VM	Lower Pleistocene	RUIZ-BUSTOS 1999
Weinan and loc A, *E. stenonis*	15	Middle-Late Villafranchian	DENG TAO com. pers., FORSTEN 1986

Table 7. Localities with primitive horses appearing in Figures 10-13, symbols, assumed age, and corresponding bibliographical references.

Huelago (n°16079, symbol Hu) is particularly long and gracile. The metacarpals of Olduvai (symbol 18) are relatively robust. Metapodials of the small horse of Vatera (symbol V2) and of Dmanisi IV and V (symbol 22) do not fit well in any group.

The combination of the index of diaphyseal depth with the index of distal flatness clearly shows two groups of third metacarpals (Figure 12). The various subspecies of *E. stenonis* are separated from the various *E. numidicus*-like forms. For the third metatarsals, the separation is still present although not as evident (Figure 13).

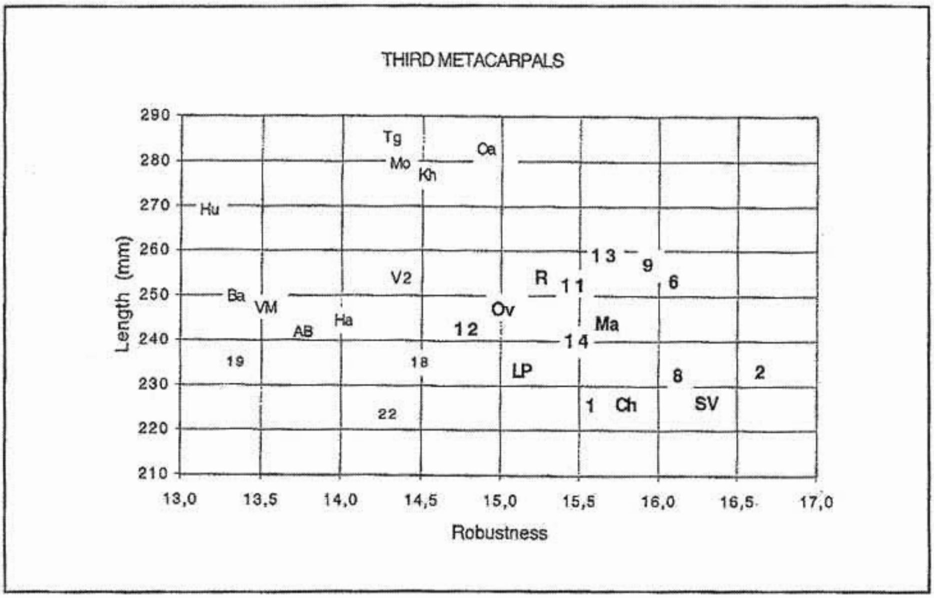

Fig. 10. Scatter diagram of metacarpal indices of robustness versus maximal length in millimeters; symbols in Table 7. *E. stenonis* in bold.

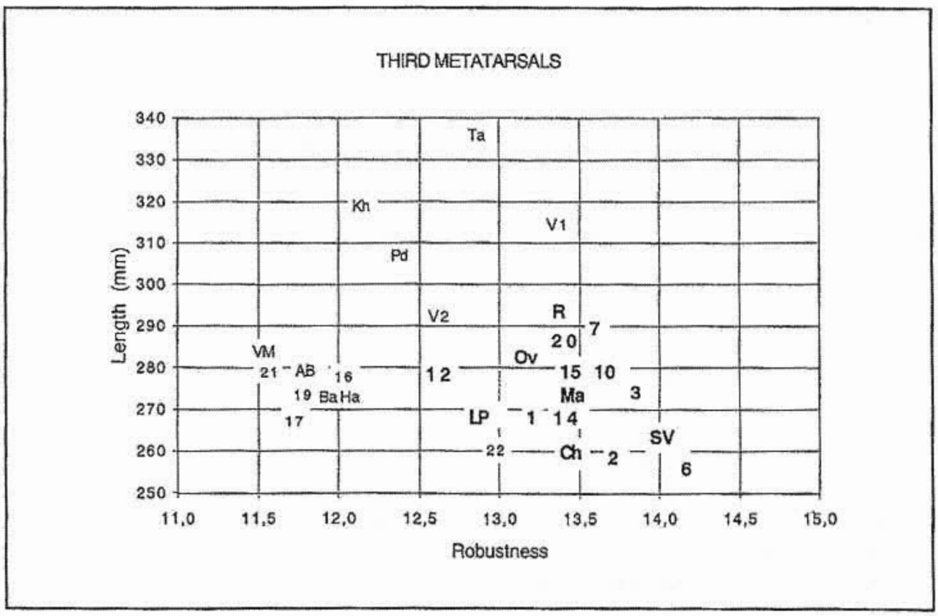

Fig. 11. Scatter diagram of metatarsal indices of robustness versus maximal length in millimeters; symbols in Table 7. *E. stenonis* in bold.

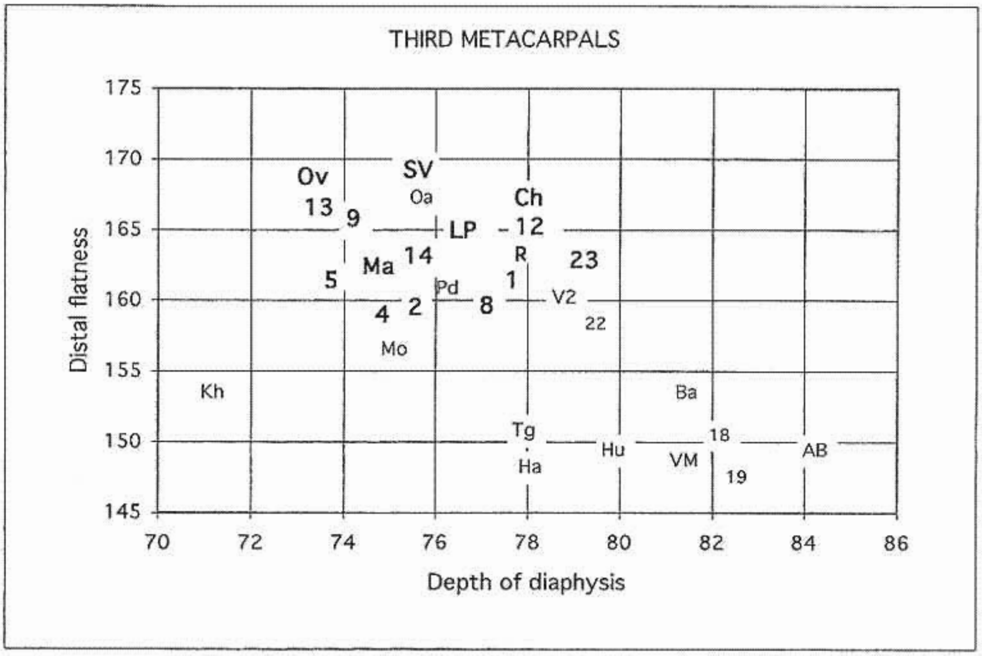

Fig. 12. Scatter diagram of metacarpal indices of diaphyseal depth versus indices of distal flatness; symbols in Table 7. *E. stenonis* in bold.

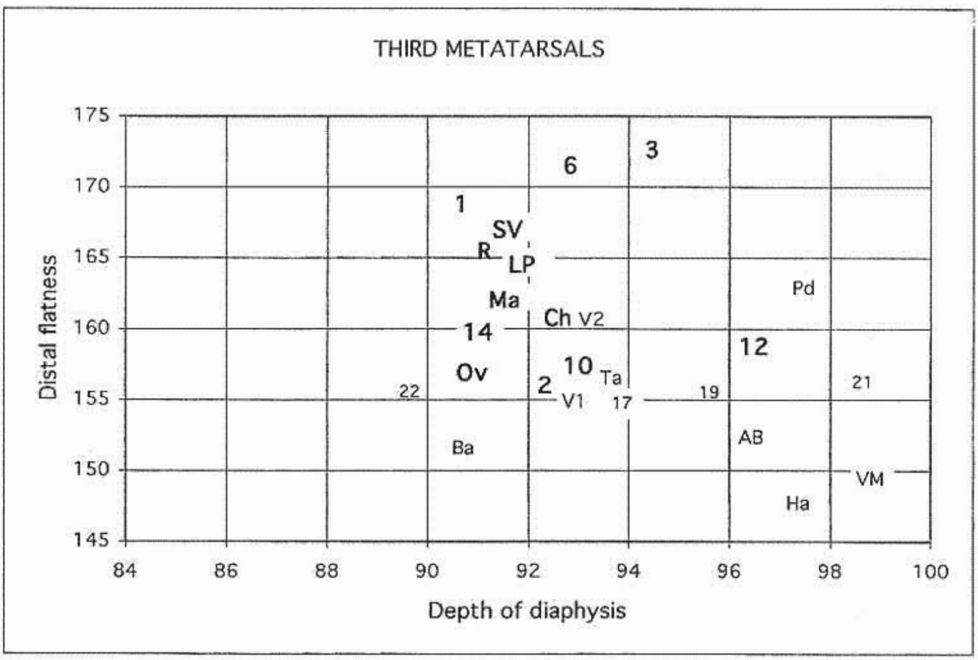

Fig. 13. Scatter diagram of metatarsal indices of diaphyseal depth versus indices of distal flatness; symbols in Table 7. *E. stenonis* in bold.

The position of the horses of Vatera is not clear. The large horse is as robust as *Equus stenonis* but much larger. The smaller horse is intermediate in robustness between *E. stenonis* and *E. numidicus*-like forms. Neither can be referred to a true *E. stenonis*. The morphology of the Vatera horses does not give any precise chronological indication. Could the very coexistence of two primitive horses be more informative?

VIII. COEXISTENCE OF TWO PRIMITIVE *EQUUS*

Some of the considered sites have yielded more than one morph. It may be because the collections of one locality include fossils from different chronological levels or because two or more equids did live together at the same time and at the same place.

It seems that in Africa, during the Pliocene and the early Lower Pleistocene, two horses did coexist at Aïn Jourdel, in the Shungura Formation of the Omo valley, in East Turkana, and at Olduvai. In Europe, the coexistence of two primitive horses is probably due to mixing of different levels at Valdarno and Senèze but may have been real at Huelago, Dmanisi, and possibly Khapry. Usually, however, only one primitive horse is found in Pliocene and early Lower Pleistocene European sites.

Later on (Pyrgos, Psekups, Ubeidiyeh, Fîntîna lui Mitilan, Cueva Victoria, Pirro, Solilhac, Cullar de Baza, Huescar, Redicicoli, Untermassfeld) and especially during the Middle Pleistocene (Akhalkalaki, Voigstedt, Süssenborn, Nalaikha, Tologoï), the coexistence of at least two *Equus* is frequent.

Thus, the heterogeneity of the Vatera material can be interpreted either as an indication of not very ancient age, or as an original feature, or as an indication of the sampling of more than one level.

IX. PRIMITIVE *EQUUS* AND PRIMITIVE CANIDS

In Europe, the replacement of *Nyctereutes megamastoides* by *Canis etruscus* is one of the events that marks the transition from the Middle to the Late Villafranchian (and/or from the Pliocene to the Lower Pleistocene, and/or from the MN 17 zone to the MN 18 zone, and/or from the Saint-Vallier Faunal Unit to the Olivola Faunal Unit).

Nyctereutes megamastoides, or *Eucyon*, without *Canis* is listed at El Rincón, Huelago, and Montopoli (ALBERDI *et al.*, 1998), Saint-Vallier (DEBARD *et al.*, 1994), La Puebla de Valverde (GAUTIER & HEINTZ, 1974), Chilhac (BOEUF, 1997), Dafnero and Sesklo (KOUFOS & KOSTOPOULOS, 1997; ATHANASSIOU, 2001), Sarikol Tepe (KOSTOPOULOS & SEN, 1999), Tetoiu (SAMSON, 1975), and at Vatera. Huelago and Vatera are the only sites where two *Equus* are associated with a *Nyctereutes*.

In presumably younger sites, two (or more) *Equus* are associated to *Canis* without *Nyctereutes*: Blassac-la-Girondie (BEDEN & GUTH, 1970), Dmanisi (VEKUA, 1995), Khapry and Livenzovka (SOTNIKOVA, 1989). At Senèze, where more than two *Equus* are represented, both *Nyctereutes* and *Canis* are listed by SCHAUB (1944).

CONCLUSIONS

Pending the discovery of better material (and in particular of skulls) the real taxonomy of primitive horses is unclear. Presently, the size combined with metapodial robustness and depths may be used to define, and attempt a distinction between, various Pliocene and Lower Pleistocene horses, and in particular true *Equus stenonis* and *Equus numidicus*-like forms.

Two horses are represented in the Vatera Formation: a large and robust form (poorly documented), and a smaller one. The smaller is about the size of the *E. stenonis* of La Puebla de Valverde, Sesklo, and El Rincón, but it is slenderer and more cursorial. The *E. stenonis* of Sarikol Tepe fits in between the bulk of Vatera smaller bones and the very large third metatarsal. Neither the smaller nor the larger bones of Vatera belong to normal *E. stenonis* or to *E. numidicus*-like forms. In the present state of our knowledge, Vatera and Huelago are the only localities in Europe where two *Equus* seem to coexist with *Nyctereutes*.

In modern times, three cases of more or less close cohabitation of equids are known: Przewalski horses and Hemiones in Mongolia, Grevy's zebras and Wild Asses in Somalia, Grevy's zebras and Plains zebras in Northern Kenya. Przewalski horses and Hemiones are both slender and cursorial forms of about the same size and it is not difficult to picture them both in the same open landscape. The three other species are very different. Grevy's zebras are the largest of the extant species of *Equus*; although their bones are slender, they are less cursorial in their proportions than Wild Asses. Plains zebras are smaller, more robust, and even less cursorial than Grevy's zebras. The overlap of the three African species is not, however, very large. According to KINGDON (1979), the Grevy's zebra 'is wedged between the arid-adapted wild ass and the water-loving *E. quagga*' (plains zebra). In the case of Vatera, the cursorial proportions of the smaller horse and their gracility would be consistent with dry conditions and open landscapes. The large form is poorly known, but its robustness would be consistent with humid conditions. Their coexistence would suggest either an ecological mosaic, or a limit position between two landscapes, or seasonal migrations.

ABSTRACT

The Variability Size Index evidences the presence of two species of *Equus* in the Vatera Formation. The characterization of Pliocene and Early Pleistocene equids on the basis of their metapodials shows that the horses of Vatera differed both from *E. stenonis* and from *E. numidicus*-like forms. The larger form of Vatera could weight as much as a small Draft horse (more than 600 Kg) and was probably adapted to humid conditions. The smaller form weighted about as much as an average Grevy's zebra (more than 400 Kg) but was higher at the withers (about 157 cm), slenderer, more cursorial, and was probably adapted to dry conditions and open landscapes. Vatera and Huelago seem to be the only localities in Europe where two horses were associated with *Nyctereutes* and not with *Canis*.

ΠΕΡΙΛΗΨΗ

Στο Σχηματισμό των Βατερών τεκμηριώνεται η ύπαρξη δύο απολιθωμένων ειδών του γένους *Equus*. Ο χαρακτηρισμός των πλειοκαινικών και κατωπλειστοκαινικών Ιππίδων βάσει της μορφολογίας των μεταποδίων τους δείχνει ότι οι ίπποι των Βατερών διαφέρουν τόσο από τον *Equus stenonis*, όσο και από τους ίππους του τύπου του *E. numidicus*. Ο μεγαλόσωμος ίππος των Βατερών υπολογίζεται ότι ζύγιζε περισσότερο από 600 κιλά και ήταν πιθανότατα προσαρμοσμένος σε υγρό περιβάλλον. Ο μικρότερος ίππος ζύγιζε περίπου όσο μια ζέβρα του Grevy (περισσότερο από 400 κιλά), αλλά ήταν ψηλότερος (ύψος στο ακρώμιο περίπου 157 εκ.), είχε πιο λεπτό σκελετό και ήταν πιθανότατα προσαρμοσμένος σε ανοιχτό και ξηρό περιβάλλον. Τα Βατερά και το Huelago φαίνεται να είναι οι μόνες Ευρωπαϊκές θέσεις όπου δύο μορφές ίππων απαντούν μαζί με *Nyctereutes* και όχι με *Canis*.

ACKNOWLEDGEMENTS

Particular thanks are for M.D. DERMITZAKIS and P.Y. SONDAAR who entrusted me with the study of the Vatera equids and invited me to a marvelous Workshop at Polichnitos. H. BRINKERIK, G. LYRAS, J. DE VOS, and R. VAN ZELST helped in many ways with the material at Vrissa and in Leiden. Personal data on Greek equids were kindly communicated by G. KOUFOS and A. ATHANASSIOU. Moreover, A. ATHANASSIOU spotted a wrong attribution of a Giraffid elbow articulation to the large *Equus* and various other mistakes in the text and captions.

REFERENCES

ALBERDI, M.T., CALOI, L. & M.R. PALOMBO (1998). Large mammal associations from the Early Pleistocene: Italy and Spain. In: The Dawn of the Quaternary. *Proceedings of the SEQS-EuroMam symposium* 1996. T. VAN KOLFSCHOTEN & P.L. GIBBARD Editors. *Medelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, 521-532, 7 fig., 3 tabl.

ALBERDI, M.-T. & A. RUIZ-BUSTOS (1989). Taxonomía y Biostratigrafía de Equidae (Mammalia, Perissodactyla) en la Cuenca de Guadix-Baza (Granada). In: Geología y Paleontología de la Cuenca de Guadix-Baza, *Trabajos sobre Neógeno-Cuaternario*, 11: 239-270, 18 tabl., 1 fig., 1 pl.

ALEKSEEV, M.N. (1997). The N/Q boundary in Asian Russia and Tadjikistan. In: *The Pleistocene Boundary and the Beginning of the Quaternary*, Edited by J.A. VAN COUVERING, *World and regional Geology* 9, Cambridge University Press: 227-231.

ATHANASSIOU, A. (2001). New data on the *Equus stenonis* from the Late Pliocene locality of Sesklo (Thessaly, Greece). *Geodiversitas*, 23 (3): 439-469.

BEDEN, M. & C. GUTH (1970). Un nouveau gisement de vertébrés du Villafranchien de la vallée de l'Allier. *C. R. Acad. Sci.*, 271: 168-171.

BOEUF, O. (1997). A propos de Chilhac, Senèze, Blassac-la-Girondie (Haute-Loire, France) gisements du Pliocène terminal, leur intérêt biochronologique. *Actes du Congrès BiochroM'97*, AGUILAR, J.-P., LEGENDRE S. & J. MICHAUX (Eds), *Mémoires et*

Travaux, E.P.H.E., Inst. Montpellier, 21: 661-668, 9 fig.

BOUCHEZ, R., LOPEZ CARRANZA, E., MA, J.-L., AMOSSE, J., PIBOULE, M., COMU, A., DIEBOLD, J., GALLAND, D., REY, P., LUMLEY, H. DE, RAMIREZ PAREJA, J.A. & C. GUÉRIN (1984). Datation par spectrométrie RPE d'émàil dentaire fossile dans le domaine de 50.000 ans à plusieurs millions d'années. *Revue d'Archéométrie*, 8: 70-79, 2 fig. 7 tabl.

BROWN, F.H., MCDOUGALL, I., DAVIES, T. & R. MAIER (1985). An integrated Plio-Pleistocene chronology for the Turkana Basin. In: *Ancestors: the hard evidence*, E. DELSON Ed.: 82-90, 2 fig., 2 tabl., Alan R. Liss, Inc., New York.

BROWN, F.H. & C.S. FEIBEL (1986). Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. *Journal of the Geological Society*, 143: 297-310.

DEBARD, E., FAURE, M. & C. GUÉRIN (1994). Stratigraphie du gisement villafranchien moyen de Saint-Vallier (Drôme). *C.R. Acad. Sci.*, 318: 1283-1286.

DE GIULI, C. (1972). On the type form of *Equus stenonis* COCCHI. *Palaeontographia italica*, 68 (n.s. 38): 35-49, 11 pl., 3 fig., 21 tabl.

DENG TAO (1997). Chinese fossils of the genus *Equus* and their reflections on the climatic changes. *Ph.D. Dissertation*. Northwest University: 150p., 20 pl., 15 fig., 37 tabl., Xi'an.

DENG TAO (1999). *Equus qingyangensis* sp. nov. (Perissodactyla, Equidae) from the Early Pleistocene of Qingyang, Gansu, China. *Vertebrata Palasiatica*, 37(1): 62-74.

DERMITZAKIS, M., EISENMANN, V. & S. GALOUKAS (1991). The presence of Pleistocene Mammals in Lesvos island (E. Aegean). *Bull. Geol. Soc. Greece* 25 (2): 405-421, 7 fig. *Proceedings of the 5th Congress of the Geological Society of Greece*, Thessaloniki, May 24-27, 1990.

DODONOV, A.E., ZHEGALLO, V.I., PENKOV, A.V. & M.V. SOTNIKOVA (1991). Stratigrafia mestonakhozhdenij pozdnepliotsenovykh pozvonochnykh Iuzhnogo Tadjikistana. Izvestia Akademii Nauk SSSR, *Serija Geologicheskaja*, 5: 12-20, 5 fig.

EISENMANN, V. (1979). Les métapodes d'*Equus sensu lato* (Mammalia, Perissodactyla). *Géobios*, 12 (6): 863-886, 19 fig., 11 tabl.

EISENMANN, V. (1984). Sur quelques caractères adaptatifs du squelette d'*Equus* et leurs implications paléoécologiques. *Bull. Mus. nat. Hist. nat.*, Paris, 4ème série, 6, section C, 2: 185-195, 3 fig., 1 tabl.

EISENMANN, V. (1999). *Equus granatensis* of Venta Micena and evidence for primitive non-stenonid horses in the Lower Pleistocene. *Proceedings of the International Conference of Human Palaeontology* "The hominids and their environment during the Lower and Middle Pleistocene of Eurasia", Orce 1995: 175-189, 9 fig., 1 pl., 6 tabl.

EISENMANN, V. (2000). *Equus capensis* (Mammalia, Perissodactyla) from Elandsfontein. *Palaeontologia africana*, 36: 91-96, 4 fig., 2 tabl.

EISENMANN, V. & M. BAYLAC (2000). Extant and fossil *Equus* (Mammalia, Perissodactyla) skulls: a morphometric definition of the subgenus *Equus*. *Zoologica Scripta*, 29 (2): 89-100.

EISENMANN, V. & A. KARCHOUD (1982). Analyses multidimensionnelles des métapodes d'*Equus*. *Bull. Mus.natn. Hist. nat.*, Paris, 4ème série, t. 4, 1-2, Section C, 75-103, 12 fig., 5 tabl.

EISENMANN, V. & P. SONDAAR (1998). Pliocene vertebrates locality of Çalta, Ankara, Turkey. 7. *Hipparion*. *Geodiversitas*, 20(3): 409-439, 21 fig., 16 tabl.

FORSTEN, A. (1982). Indices in equid systematics and phylogeny. *Annales Zool. Fennici*, 19: 183-191.

FORSTEN, A. (1986). Chinese fossil horses of the genus *Equus* . *Acta Zoologica Fennica*, 181: 1-40, 36 fig., 5 tabl.

FORSTEN, A. (1998). The fossil horses (Equidae, Mammalia) from the Plio-Pleistocene of Liventsovka near Rostov-Don, Russia. *Géobios*, 31 (5): 645-657.

GABUNIA, M.K. & A.K. VEKUA (1989). Antropogenovye loshadi Gruzii. Akademija Nauk Gruzinskoj SSR, Institut Paleobiologii im. L. Sh. Davitashvili, 140pp, 28 fig., 8 pl., 18 tabl. Metsniereba, Tbilisi.

GABUNIA, M.K. & A.K. VEKUA (1995). A Plio-Pleistocene hominid from Dmanisi, East Georgia, Caucasus. *Nature*, 373: 509-512.

GAUTIER, F. & E. HEINTZ (1974). Le gisement villafranchien de La Puebla de Valverde (Province de Teruel, Espagne). *Bulletin du Muséum National d'Histoire Naturelle*, Sciences de la Terre, 36, 228: 113-136.

GERAADS, D., HUBLIN, J.-J., JAEGER, J.-J., TONG, H., SEN, S. & P. TOUREAU (1986). The Pleistocene hominid site of Ternifine, Algeria: new results on the environment, age, and human industries. *Quaternary Research*, 25: 380-386, 3 fig.

GROMOVA, V.I. (1949). Istorija loshadej (roda *Equus*) v Starom Svete. Chast' 1. Obzor i opisanie form. *Trudy paleont. Inst., Akad. Nauk SSSR*, 17 (1): 373p., 53 fig., 8 pl., 20 tabl.

HEINTZ, E. (1970). Les Cervidés villafranchiens de France et d'Espagne. *Mémoires du Muséum national d'Histoire naturelle*, C, XXII, 2 volumes.

KINGDON, J. (1979). *East African mammals. An atlas of evolution in Africa*. Academic Press, Volume III B. Equids: 120-179.

KOSTOPOULOS, D.S. & S. SEN (1999). Late Pliocene (Villafranchian) mammals from Sarikol Tepe, Ankara, Turkey. *Mitteilungen Bayer. Staatsslg. Paläont. hist. Geol.*, 39: 165-202.

KOUFOS, G.D. & D.S. KOSTOPOULOS (1993). A stenonoid horse (Equidae, Mammalia) from the Villafranchian of Western Macedonia (Greece). *Bull. Geol. Soc. Greece*, 28(3): 131-143, 4 fig., 2 pl., 5 tabl.

KOUFOS, G.D. & D.S. KOSTOPOULOS (1997). Biochronology and succession of the Plio-Pleistocene macromammalian localities of Greece. *Actes du Congrès BiochroM'97*, AGUILAR, J.-P., LEGENDRE S. & J. MICHAUX (Eds), *Mémoires et Travaux, E.P.H.E., Inst. Montpellier*, 21: 619-634, 4 fig.

LUNDELIUS, E.L. Jr., CHURCHER, C.R., DOWNS, T., HARINGTON, C.R., LINDSAY, E.H., SCHULTZ, G.E., SEMKEN, H.A., WEBB, S.D. & R.J. ZAKRZEWSKI (1987). The North American Quaternary sequence, In: *Cenozoic Mammals of North America, Geochronology and Biostratigraphy*, M.O. WOODBURNE Ed., 211-235, 3 fig., Univ. of California Press.

MEADOW, R.H. (1986). Some Equid Remains from Cayönü, Southeastern Turkey. In: MEADOW, R.H. & H.P. UERPMANN (eds). *Equids in the ancient world. Beihefte zum Tübinger Atlas des Vorderen Orients*, Reihe A: 266-301, 3 fig., 7 tabl., Wiesbaden.

MEADOW, R. (1999). The use of size index scaling techniques for research on archaezoological collections from the Middle East. In: *Historia Animalium ex Ossibus. Festschrift für Angela VON DEN DRIESCH zum 65. Geburtstag*, 285-300. *Internationale Archäologie*, Bd 8: Studia honoraria. Verlag Marie Leidorf, Rahden, Westf.

RADULESCO, C. & P. SAMSON (1990). The Plio-Pleistocene Mammalian succession of the Olteţ Valley, Daciq Basin, Romania. *Quartärpaläontologie* 8, 225-232. Berlin.

RUIZ BUSTOS, A. (1999). Biostratigraphy of the continental deposits in the Granada, Guadix, and Baza Basins (betic Cordillera). *Proceedings of the International Conference of Human Palaeontology* "The hominids and their environment during the Lower and Middle Pleistocene of Eurasia", Orce 1995: 153-174, 2 fig., 1 tabl.

SAMSON, P. (1975). Les Equidés fossiles de Roumanie. *Geologica Romana,* 14: 165-352.

SCHAUB, S. (1944). Die oberpliocaene Säugetierfauna von Senèze (Haute-Loire) und ihre verbreitungsgeschichtliche Stellung. *Ecl. Geol. Helv.*, 36: 270-289.

SOTNIKOVA, M.V. (1989). Khishchnye Mlekopitaiushchie Pliotsena - Rannego Pleistotsena. Akad. Nauk SSSR, Ordena trudovogo krasnogo znameni Geologicheskij Institut, Trudy 440, Izd. Nauka, Moskva, 121pp.

TAMRAT, E., THOUVENY, N., TAÏEB, M. & N.D. OPDYKE (1995). Revised magnetostratigraphy of the Plio-Pleistocene sedimentary sequence of the Olduvai Formation (Tanzania). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 114: 273-283.

TORRE, D. (1987). Pliocene and Pleistocene marine-continental correlations. *Proceedings of the VIIIth RCMNS Congress, Ann. Inst. Geol. Publ. Hung*, 30: 71-77, 2 fig., Budapest.

TORRE, D., ALBIANELLI A., BERTINI A., FICCARELLI G., MASINI, F. & G. NAPOLEONE (1996). Paleomagnetic calibration of Plio-Pleistocene mammal localities in central Italy. *Acta zool. cracov.*, 39 (1): 559-570, 6 fig.

UERPMANN, H.P. (1982). Faunal remains from Shams ed-din Tannira, a Halafian Site in Northern Syria. *Beyrutus* 30: 3-52.

VALLI, A. (2000). Le gisement villafranchien moyen de Saint-Vallier (Drôme): étude taphonomique; paléontologie des Cervidae et des Bovinae. *Thèse*.

VEKUA, A.K. (1995). Die Wirbeltierfauna des Villafranchium von Dmanisi und ihre biostratigraphische Bedeutung. *Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz*, 42: 77-180.

WESTERHOFF, W.E., CLEVERINGA, P., MEIJER, T., VAN KOLFSCHOTEN, T. & W.H. ZAGWIJN (1998). The Lower Pleistocene fluvial (clay) deposits in the Maalbeek pit near Tegelen. In: The Dawn of the Quaternary. *Proceedings of the SEQS-EuroMam symposium 1996.* KOLFSCHOTEN, T. VAN & P.L. GIBBARD Editors: *Medelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, 35-69, 16 fig., 1 pl. 6 tabl.